

## Algal Succession in a *Macrocystis pyrifera* Forest

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### Abstract

Algal succession within a subtidal forest of the giant kelp *Macrocystis pyrifera* was studied by following colonization and community development on concrete blocks fastened to the bottom. Sets of blocks were placed in the bed at 3-month intervals. Subsequent algal development on each set was followed for over a year. All macroscopic species attached to the substrata were noted, and the number and length of basal branches determined every 1 to 3 months. Colonizing plants fell into 3 categories: rapid-growing ephemerals, and rapid and slow-growing perennials. Ephemerals such as *Giffordia* (*Ectocarpus*) *mittelliae*, *Colpomenia peregrina*, and diatom films generally produced an initial bloom on the blocks but were gradually replaced by perennials (articulated corallines, *Rhodomenia* spp., *Gigartina* spp.) characteristic of the mature kelp community. These stages, rather than representing "ecological" succession, seemed to reflect differences in growth rate and success in interspecific competition for space and light. Colonization on the blocks varied with season, indicating that most species have either a spring-summer or fall-winter period of maximum reproduction. *M. pyrifera* sporophyte colonization was greatest in spring. During community development, algal diversity ( $H$ ), number of species ( $s$ ) and evenness ( $J$ ) all reached a peak within 100 to 200 days regardless of the time the blocks were started. Diversity and number of species then fell as ephemeral species disappeared. These species were apparently unable to compete with perennials and, once gone, did not recolonize. Evenness remained high.

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### Introduction

Studies of succession have been used to describe changes of many community characteristics through time, including population interactions, energy flow, nutrient cycling, and community composition. The underlying supposition is that information gained from studying a particular community characteristic (or group of characteristics) through time will yield information not only on interactions during development, but will give insights into the dynamics of mature communities. Factors apparently affecting the processes observed can then be investigated by experiment. Such an approach has been used by Dayton (1971) in rocky intertidal communities.

Succession has also become a sub-discipline in itself as various workers have proposed characteristics unique to it. Observed sequential changes in com-

munity composition through time have produced the hypothesis of "true," "ecological," or "biotic" succession during which early communities modify the environment, creating conditions which cause their own replacement while favoring the invasion of species associated with later communities (Clements and Shelford, 1939). Keever (1950), in one of the few studies designed to test this hypothesis in terrestrial communities, found that the early stages of old field succession result from differences in seed germination and growth and reproductive characteristics of invading species. These differences had a greater influence on the early successional sequence than environmental changes produced by the plants.

The causes of succession in intertidal plant communities are also controversial. Some investigators (Hatton, 1932; Bokenham and Stephenson, 1938;

Rees, 1940; Northcraft, 1948) have suggested that early, ephemeral colonists enhance the establishment of perennials. However, Lee (1966) concluded that developmental patterns result from differences in morphology, phenology, and success in competition for space; not from environmental changes produced by preceding stages. Connell (1972) could find no convincing evidence that early colonizers enhance the establishment of later dominants, and suggested that community or biological control occurs after the dominants become established and alter the physical environment, allowing other species to enter the community.

Some of the controversy discussed above arises from individual interpretations of the meaning of the term "succession". In order to clearly separate the phenomenon from the causes, the term succession as used herein will mean only changes in community composition through time, without any implication of cause.

In addition to possible interactions between stages, a variety of community characteristics seem to show trends during succession (Margalef, 1963; Odum, 1969). Trends in diversity and its components have been of particular interest since they may indicate changes in community stability, niche utilization, and biological interactions (Pielou, 1966a; Auclair and Goff, 1971; Reiners *et al.*, 1971; Whittaker, 1972). Odum (1969) states that both the number of species and equitability usually increase during succession. In contrast, Auclair and Goff (1971) show a general decrease in diversity during the terminal stages of terrestrial forest succession which results from the monopolization of resources by a few species. Diversity trends during succession in benthic marine communities have not been examined in detail. Studies which have been done suggest that the degree of predation (Paine, 1966) and physical rigor (intense wave action, Grigg and Maragos, 1974) may have a strong influence on these trends if a competitive dominant exists in the community which is capable of monopolizing available space.

Although relatively unexplored, *Macrocystis* spp. forests are excellent environments for experimental studies of community development. The vegetation is often rich in species and structurally complex, and related work discussed below indicates that community development can be relatively rapid compared with secondary succession on land. However, quantitative succession studies within this environment have not previously been undertaken. North (1971) reports

variations in the density of *Macrocystis* spp. in some forests, and has observed colonization of areas within forests which were previously grazed by sea urchins. Colonization and subsequent development seemed to be a chance phenomenon depending on algal spores present at the time of urchin removal, and the ability of certain plants to shade-out others. Clarke and Neushul (1967) state that "ecological" succession can occur in these forests but give no supporting data. The subtidal studies of Wilson (1925), Coe (1932), Coe and Allen (1937), Aleem (1957), and Fager (1971) were designed to investigate various aspects of colonization and community development on either panels of various materials suspended from a pier inshore from *Macrocystis* spp. forests, or structures placed on a sandy bottom within 2 km of kelp forests. Since colonization of new substrata is a function of the distance of the substrata from populations of potential colonizers (Hutchins, 1952), it is difficult to predict possible events and interactions on substrata within *Macrocystis* spp. forests from these studies.

The purpose of the primarily descriptive study presented in this paper was to determine algal succession trends within a *Macrocystis pyrifera* forest and to investigate the influence of seasonality on these trends. Another paper (Foster, 1975) experimentally examines the influence of substratum roughness, competition for light, plant versus plant, and plant versus animal competition for space, grazing, and predation on sessile animals on the development of this algal community.

#### Study Site

The study was carried out in a *Macrocystis pyrifera* forest at Coches Prietos Cove on the south side of Santa Cruz Island off the coast of southern California, USA (Fig. 1). The forest grows on a rocky reef at the mouth of the cove. A schematic view of a cross section of the site is shown in Fig. 2A. To minimize possible variation due to different physical and biological conditions associated with differences in bottom topography, all experiments and sampling were carried out in a relatively level area on the south side of the reef at a depth of approximately 7.5 m below Mean Lower Low Water (MLLW). The bottom is hard volcanic cobble conglomerate (Weaver, 1969). Water motion over the reef can be very great, particularly during periods of south swell. A thermocline has never been observed over the site. *In situ*

mean temperatures vary from a maximum in August-September of 18°C to a minimum of 12°C in February-March (Barilotti and Silverthorne, 1972).

Qualitative comparisons with other *Macrocystis* spp. forests (Dawson *et al.*, 1960; McLean, 1962; Foster, personal observation) indicate that the biota on the reef, although relatively rich in algal species, is similar to that found along the Pacific Coast from Washington to northern Pacific Baja California. Using a modification of the plant form-layer system suggested by Neushul (1971), 4 algal layers can be distinguished in the study area. As shown in Fig. 2B, the canopy over the area (Layer 4) is composed of *Macrocystis pyrifera* with a surface cover of between 50 and 100%. A second layer (Layer 3), forming an understory canopy at a distance of between 0.5 and 1 m from the bottom, is composed of *Eisenia arborea* and *Laminaria farlowii*, whose blades move back and forth with surge over the plants beneath. *M. pyrifera* sporophylls are also part of this layer. Layer 2 is composed primarily of red algae, including articulated corallines, *Rhodymenia* spp., *Gelidium* spp., *Gigartina corymbifera*, and *Nienburgia andersoniana* (latter not shown in Fig. 2B). These plants extend up to 0.5 m off the bottom, but are overtopped by Layer-3 plants when present. Although not shown in Fig. 2B, vegetative branches of *Cystoseira osmundacea* also occur in this layer, while reproductive branches occur in Layers 3 and 4. Layer 1 is composed of small crustose and turf-forming species, mainly *Cladophora graminea* and various crustose corallines. Kühnemann (1970) has described a similar 4-layered vertical structure in *M. pyrifera* forests along the coast of Argentina.

#### Materials and Methods

In order to compare various experimental successional communities with the surrounding mature community, the bottom in the study area was sampled to determine per-cent cover. Sampling was carried out from September to November, 1970. A 6 x 6 m area of the bottom, with the platforms used for the succession experiments in the center, was marked off with metal tapes. Forty random points were selected within this area to determine the location of the sampling device. The sampling device consisted of a 1-m long metal bar with 1-m lengths of heavy twine attached at each end. Knots were tied in the twine every 20 cm. At each random point, the bar was placed perpendicular to one of the tapes so that at all points the

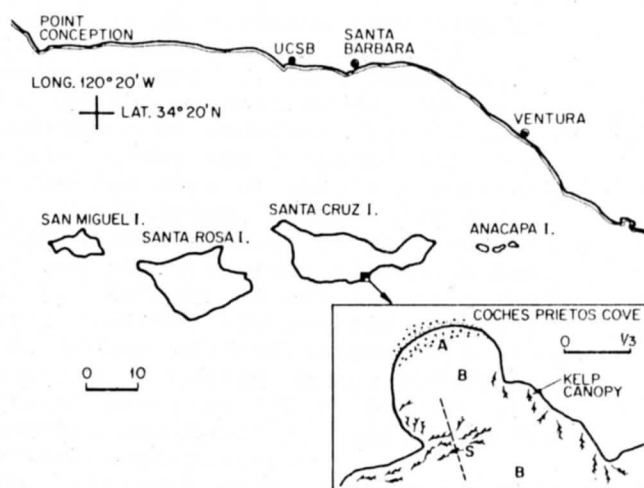


Fig. 1. Map showing location of study site at Santa Cruz Island. Insert is close-up view of Coches Prietos Cove showing location of *Macrocystis pyrifera* forests. UCSB: University of California, Santa Barbara; A: sand beach (non-dotted shore areas are rock); B: sand bottom; S: location of study site; dashed line: location of cross-section shown in Fig. 2A. Scales in km

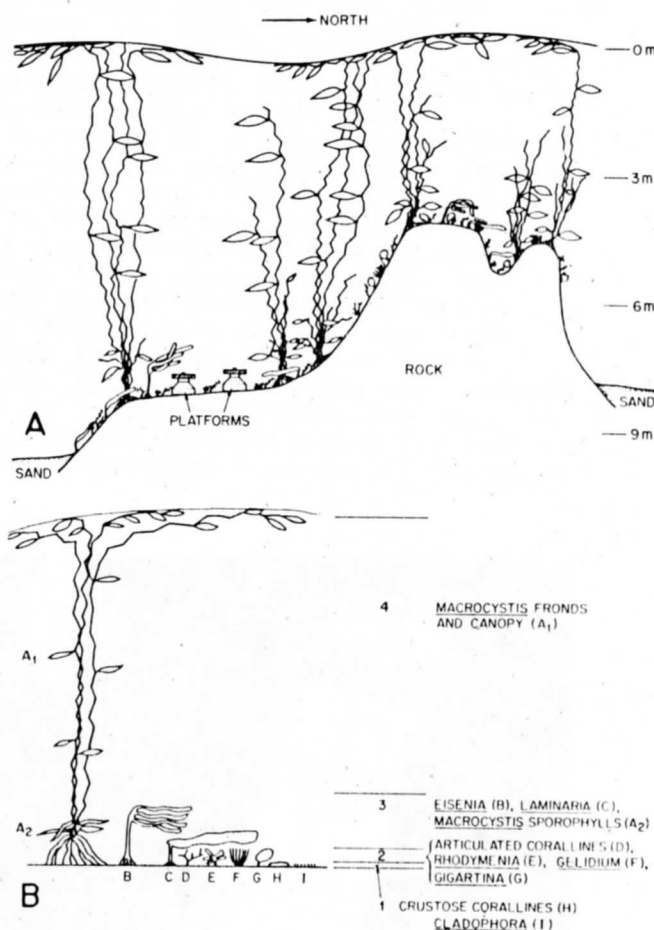


Fig. 2. (A) Cross-section of study site; horizontal scale compressed. (B) Vertical layers of subtidal vegetation. For full specific names see Table 1



bar was parallel. Nine samples were taken per random location by matching up the end knot on one piece of twine with successive knots on the other piece and recording what was beneath. This procedure eliminated the problem of trapping multiple layers of vegetation under an enclosed frame. However, the vegetation layering still presented a problem since the knots could fall on the blade of a Layer 3 plant which could have two layers of vegetation, sessile animals, rock, etc. underneath. For ease and consistency, it was decided to treat the community as if it were sheared off just above Layer 2, removing the branches of Layers 3 and 4. If the knots fell on a Layer-2 branch and another organism was beneath it, this organism was the sample. If the knots fell on a Layer-2 branch with no organisms beneath it (sand or bare rock), the Layer-2 plant was the sample. Layer 3 and 4 plants were counted only if the knots fell on their holdfasts. This procedure biases towards Layer-2 plants, but it is felt that the bias is minimal because of the almost 100% cover of holdfasts attached to the substratum. Organisms from the samples not identifiable in the field were collected for later identification. Epiphytes were not sampled.

Successional events were observed on removable concrete construction blocks (20 x 9 x 4 cm) fastened to the tops of low platforms anchored to the bottom (Fig. 3A, B). The blocks were composed of cement, sand, and gravel with a particle size of 0.5 to 5 mm. This mixture was selected to simulate the texture of the surrounding rock. Although MacGinitie and MacGinitie (1968, p. 91) imply that cement is toxic by suggesting that concrete substrata should be soaked for 6 months before use in the intertid-

al, there is no evidence that such substrata are toxic in the subtidal (Pomeroy and Weiss, 1946; Kawashima, 1972). In the present study, species composition and abundance on one set of concrete blocks was compared with that on a cleared area of natural substratum near the platforms. Composition and abundance were similar on both substrata at 39 and 96 days after placement and clearing. Between 96 and 146 days the natural clearing was covered with sand and no longer studied. Algae were always present in abundance on the blocks at the first sampling (20 to 50 days after placement, see Table 2), and there was no evidence of toxicity.

The platforms were constructed of large concrete "parking lot" bumpers (ca. 19 x 10 x 80 cm with longitudinal reinforcing rod inside) with redwood boards 3.9 x 8.8 x 127 cm bolted to the top (Fig. 3A). The redwood had stainless-steel bolts projecting through the upper surface for the attachment of the blocks. The platforms were anchored to the bottom over reinforcing rods placed in holes drilled into the rock. After placement over the rods, the platforms and rods were cemented to the bottom with underwater cement. Four platforms were installed within a 9-m<sup>2</sup> area.

Replicates of 3 blocks were fastened haphazardly to the platforms at approximately 3-month intervals beginning in March, 1970. Blocks started in March, 1970 are referred to below as spring blocks, those started in June, 1970 as summer blocks, those started in September, 1970 as fall blocks, and those started in January, 1971 as winter blocks. Each set of blocks was analyzed at 1 to 3-month intervals for over 400 days. Blocks were collected for analysis by unbolting them from the platforms and

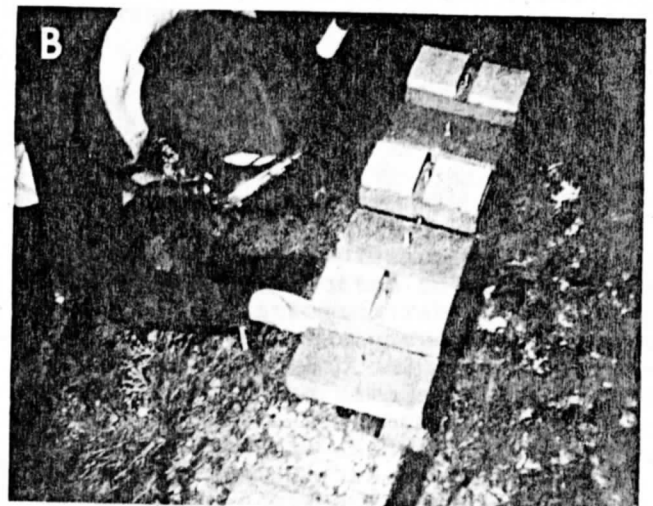
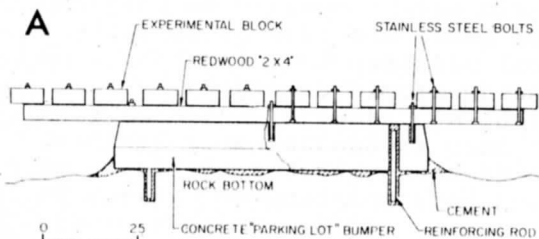


Fig. 3. (A) Platform arrangement used to hold experimental blocks; scale in cm. (B) Blocks in place underwater; blocks shown were used in studies not discussed in this paper. Blocks are 20-cm long

transferring them to the shore or to a boat in large tubs of seawater. Analysis was done in the tubs on the surface. The blocks were then replaced on the platforms. During this process care was taken to minimize disturbance of the block surfaces. The blocks were shaded and the water frequently changed to keep temperatures close to those at the platforms. In a few instances sampling was performed *in situ* when plant growth (large *Macrocystis pyrifera*) on the blocks prevented transfer without damage.

Determination of plant species, abundance, and length of basal branches was accomplished by counting all species present and the abundance and length of basal branches in 4 x 5 cm (20 cm<sup>2</sup>) quadrats placed on the tops of the blocks. Branches were considered basal if their proximal ends were located within approximately 3 mm of the substratum. Secondary branches occurring above this plane were not counted as individuals, the individual in these cases being the whole branch system. The length of these individual branch systems was measured as the distance from the substratum to the tip of the longest branch. Basal branches were counted because many of the algae have rhizomes which produce upright branches, making it impossible to distinguish individuals. In addition, a covering of sessile animals and detritus frequently made it impossible to determine whether two or more branches came from the same holdfast system.

Two areas were analyzed on each block. The quadrats were positioned over the long axis of the block, 2 cm away from the ends. These two positions were selected to reduce variation resulting from differential colonization on the edges of the blocks (Foster, 1975). The data from each of the 6 quadrats obtained per set of 3 blocks on a particular date are considered independent. Analyses of variance using diversity ( $H$ ) at successive analysis times as treatments and pairs of quadrats from the same substratum as blocks showed no significant block effects. In addition, quadrats from half-block controls showed no significant differences in diversity or species composition from full-sized blocks (Foster, 1975).

Some algae, particularly the corallines, were difficult to identify when small. This resulted in more species lumping (fewer species noted than actually present) during the early stages of succession than the later, and lowers the diversity in the data analysis for the early stages.

Small filamentous algae often covered extensive areas within the quadrats, and

counting their basal branches was difficult. As an alternative to direct counts, per-cent cover within the quadrats was estimated by eye. Per-cent cover was converted to basal branches (abundance) using conversion factors based on counting branches present in area of known size with 100% cover. The conversion factors used were: *Pterosiphonia dendroidea*, *Herposiphonia plumula*, and *Pleonosporium vancouverianum* - 10% quadrat cover (2 cm<sup>2</sup>) = 30 branches; *Ceramium gardneri* - 10% quadrat cover = 20 branches; *Giffordia* (*Ectocarpus*) *mittellae* - 10% quadrat cover = 10 branches. Diatom films were left as per-cent cover.

The diversity ( $H$ ) for the plants in each 20-cm<sup>2</sup> quadrat was calculated using Brillouin's (1962) formula:

$$H = [1/N] \log_2 [N! / N_1! N_2! \dots N_s!],$$

where  $H$  is the diversity in bits per individual (basal branch),  $N$  is the total number of basal branches,  $N_i$  is the number of basal branches belonging to the  $i$ th species, and  $s$  is the total number of species. As pointed out by Pielou (1966b), this is the preferred measure when collections are small enough for all members to be identified and counted. Evenness ( $J$ ) for each quadrat was calculated using a modification of the formula given by Pielou (1966b) where

$$J = H/H_{\max},$$

and

$$H_{\max} = [1/N] \log_2 [N! / (N/s!)^s].$$

The term for the non-integer part of  $N/s$  was excluded for ease of calculation. Diversity and evenness were calculated with the aid of the tables in Lloyd *et al.* (1968).

Additional data were obtained from underwater color photographs of the blocks taken at times when they were not directly analyzed. Small samples of species which could not be identified in the field were removed from areas outside the quadrats for later identification.

## Results

### The Surrounding Community

A total of 360 samples were used to assess per-cent bottom cover in the area around the platforms (Table 1). The species versus samples curve began to level off before 200 samples were taken, indicating that the sample size was adequate (Fig. 4). The corallines *Calliarthron cheilosporoides* and *Corallina officinalis* var. *chilensis* are by far the most common algae. Layer 2 covers the great-

Table 1. Bottom cover of the community around the experimental platforms. Species listed in order of coverage. N = 360

Species	No. of samples containing species	% cover	Layer no. <sup>a</sup>
<b>Algae</b>			
<i>Calliarthron cheilosporiodes</i>	97	26.9	2
<i>Corallina officinalis</i> var. <i>chilensis</i> <sup>b</sup>	70	19.4	2
<i>Lithophyllum</i> spp. <sup>c</sup>	31	8.6	1
<i>Bossiella orbigniana</i> spp. <i>orbigniana</i>	23	6.4	2
<i>Rhodymenia californica</i>	17	4.7	2
<i>Nienburgia andersoniana</i>	13	3.6	2
<i>Rhodymenia californica</i> var. <i>attenuata</i>	11	3.1	2
<i>Gelidium robustum</i>	9	2.5	2
<i>Cystoseira osmundacea</i>	7	1.9	2 <sup>d</sup>
<i>Cladophora graminea</i>	7	1.9	1
<i>Gelidium nudifrons</i>	6	1.7	2
<i>Laminaria farlowii</i>	5	1.4	3
<i>Macrocystis pyrifera</i>	4	1.1	4
<i>Tiffaniella synderae</i>	3	0.8	1
<i>Fauchea laciniata</i>	2	0.6	1
<i>Zonaria farlowii</i>	2	0.6	2
<i>Gigartina corymbifera</i>	2	0.6	2
<i>Lithothrix aspergillum</i>	2	0.6	2
<i>Acrosorium uncinatum</i>	2	0.6	1
<i>Plocamium cartilagineum</i>	2	0.6	2
<i>Rhodymenia pacifica</i>	2	0.6	2
<i>Botryocladia pseudodichotoma</i>	1	0.3	2
<i>Eisenia arborea</i>	1	0.3	3
<i>Halidrys dioica</i>	1	0.3	2
<i>Opuntiella californica</i>	1	0.3	2
<i>Schizymenia dawsonii</i>	1	0.3	2
<b>Non-algae</b>			
Hydroids	1	0.3	
Sand	30	8.3	
Rock	7	1.9	
<b>Total</b>	<b>360</b>	<b>100</b>	

<sup>a</sup>See Fig. 2B.

<sup>b</sup>Also includes *Serraticardia macmillani* and *Halyleptilon gracilis*. These three species were not easily distinguished from each other but are present in the area. *C. officinalis* var. *chilensis* was by far the most abundant.

<sup>c</sup>Primarily *Lithophyllum imitans* and *Phymatolithom lenormandii*.

<sup>d</sup>Can become part of Layer 4 when reproductive in summer.

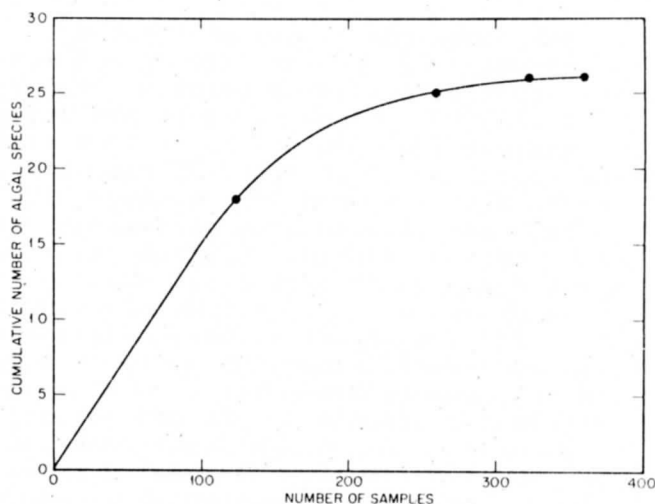


Fig. 4. Cumulative number of species versus number of samples from the community survey.

est bottom area (74.4%) and, counting all species and varieties listed in the footnote in Table 1 as different species, contains the greatest number of plant species (20). The area contains species from both the upper and mid-subtidal zones as described by Neushul (1965).

Sand (8.3% cover) is associated with small depressions in the highly irregular rock bottom. The distribution of sand over the area varies depending on the magnitude of water motion which shifts the sand around, covering and uncovering small areas of rock. This sand movement can affect community composition by opening up small areas for colonization and by acting as a selective agent for those species which can withstand burial (Dahl, 1971; North, 1971; Rosenthal et al., 1974). Space also becomes available when adult *Macrocystis pyrifera* and other plants are torn loose from the bottom during periods of heavy swell (ZoBell, 1971; Rosenthal et al., 1974). This process of exposing new substrata for colonization has also been observed by Kitching (1937) in *Laminaria* spp. forests.

Aside from the vegetational changes noted above, there seemed to be little seasonal variation in the larger or more conspicuous plants. Although the bottom survey was done in the fall, qualitative observations of the area over a 3-year period at all times of the year indicate little variation other than a summer period of colonization by *Colpomenia peregrina*, which is gone by September. The majority of plants in Table 1 appear to be perennials. Individual *Eisenia arborea*, *Laminaria farlowii*, *Macrocystis pyrifera*, *Geli-*

*dium* spp., and *Calliarthron cheilosporiodes* have been observed in the same locations near the platforms for over 2 years, indicating they can live at least that long. Elongation rates discussed below indicate many of the plants, particularly the articulated corallines, may be over 10 years old.

Sessile invertebrates are conspicuous by their absence (Table 1). Bryozoans, tunicates, sponges, and coelenterates, abundant in crevices and steep slopes nearby (Foster, 1972a), are generally found only as small epiphytes in the study area. Mobile invertebrates include the sea-stars *Pisaster giganteus* and *Patiria miniata*, the sea-urchin *Strongylocentrotus franciscanus*, and the abalones *Haliotis rufescens* and *H. corrugata*. Fishes are abundant.

#### Seasonal Colonization and Succession

Most investigations of intertidal algal succession have emphasized the importance of the growth and reproductive characteristics of colonizing plants in producing some of the characteristic successional stages observed. The importance of these characteristics was also apparent during this subtidal study and an attempt was made to classify all the plants found on the blocks into 3 basic growth/reproductive types: (1) ephemerals with rapid growth; (2) perennials with rapid growth; (3) perennials with slow growth. Plants which persisted on the blocks for less than 1 year, during which time they attained their adult length and/or reproductive maturity were classified as ephemerals. Plants which persisted for more than 1 year and reached mature length and/or reproductive maturity in less than 1 year were classified as rapid-growing perennials. Slow-growing perennials were those plants which persisted for more than 1 year but did not grow to their mature length or reach reproductive maturity during the first year. Plants which were known perennials (either from observations of their persistence on the blocks or in the surrounding community, or from other studies) but whose elongation rates or time to reproductive maturity could not be determined were classified as perennials, unknown growth. All others were classified as unknown. Northcraft (1948) used similar categories for intertidal algae, but listed the slow-growing perennials as late colonizers. This categorization was inappropriate for the perennials found in this study.

The complete branch abundance data from the quadrat counts, with species listed according to growth/reproductive type, are given in Foster (1972b). The data for the most common species are summarized in Table 2. Colonization was rapid whenever the blocks were started, and ephemerals were usually the most abundant early colonizers. On the spring blocks the first understory stage was a *Giffordia mitchellae* - *Colpomenia peregrina* association (50 to 150 days), followed by a *Gigartina* spp.-corallines-*Pterosiphonia dendroidea*-*Herposiphonia plumula* association. On the summer blocks, the stages were *Giffordia mitchellae* to *C. peregrina*-*Faucheia laciniata*-*P. dendroidea* to *F. laciniata*-*Rhodymenia californica*-*P. dendroidea* - corallines, then *F. laciniata* disappeared. The initial *Giffordia mitchellae* stage was absent on the fall blocks, being replaced by an early diatom film. This film was followed by a *P. dendroidea*-*F. laciniata* bloom and the perennial association. *Macrocystis pyrifera* and *Laminaria farlowii* sporophytes, along with a diatom film made up the early association on the winter blocks, followed by a *G. mitchellae* bloom and then the perennial association which included *M. pyrifera* and *L. farlowii* from the early association (Tables 2, 3).

As Table 2 shows, there was considerable variation both in species present and abundance during succession, depending upon the time of year the blocks were started. For example, *Giffordia mitchellae* and *Colpomenia peregrina* are the earliest and most abundant colonizers on spring and summer blocks, but are virtually absent at all times on fall blocks. Moreover, these algae did not appear on winter blocks, started in January, until March (73 days). Furthermore, two sets of blocks with similar initial plant composition (*G. mitchellae* and *C. peregrina* on spring and summer blocks) can have different associations developing later (*Gigartina* spp.-corallines-*Pterosiphonia dendroidea* - *Herposiphonia plumula* on spring blocks, *Rhodymenia californica*-*P. dendroidea*-corallines on summer blocks).

This seasonal aspect of colonization is shown in Fig. 5. The colonization times were determined by noting the time of the first occurrence of a particular species. The increase of a species after initial colonization was classified as new colonization only if the later plants appeared to be new individuals and not new branches arising from old plants. Most of the abundant colonizers, whether ephemerals or perennials, have either a spring - summer or fall - winter period of maximum colonization. *Macrocystis pyrifera*, the most abundant organism



Table 2. Branch abundance data for 9 most common species found on blocks. Abundance of each species in first and last analyses on each set of blocks is given as mean no. of basal branches/20 cm<sup>2</sup> (N=6)

Species	Blocks, and time in sea (days)							
	Spring		Summer		Fall		Winter	
	50 <sup>a</sup>	540	39	440	50	472	20	435
<b>Ephemerals</b>								
<i>Colpomenia peregrina</i>	2.0	0	1.5	0	0	0	0	0
Diatom film <sup>b</sup>	0	0	0	0	43	0	100	0
<i>Fauchea laciniata</i>	0	0	0	pd	P	P	0	P
<i>Giffordia mitchellae</i>	67.5	0	92.5	0	0	0	0	0
<i>Herposiphonia plumula</i>	0	12.5	0	0	0	0	0	P
<b>Perennials, rapid growth</b>								
<i>Pterosiphonia dendroidea</i>	0	2.2	P	128.0	0	52.5	0	7.2
<i>Rhodymenia californica</i>	0	0	0	10.5	0	5.1	0	P
<b>Perennials, slow growth</b>								
Corallines	0	8.0	1.5	1.7	15.5	1.3	0	P
<i>Gigartina</i> spp.	0	4.0	0	1.0	0	5.7	0	1.3

<sup>a</sup>N=2.

<sup>b</sup>Abundance in % cover.

<sup>c</sup>Most abundant on intermediate sampling dates.

<sup>d</sup>P: Present, but mean abundance < 1.

Table 3. *Macrocystis pyrifera* colonization. Data are total number of sporophytes in 10 cm long or less per set of 3 blocks. A blank indicates blocks not yet in place or no longer in place. N = blocks in place but *M. pyrifera* not counted

Blocks	Date started	Date sampled											
		1970				1971				1972			
		May	July	Sept.	Nov.	Jan.	Mar.	May	July	Sept.	Nov.	Jan.	Mar.
Spring	Mar. 1970	116 <sup>a</sup>	5	0	0	0	0	0	0	0			
Summer	June 1970		N	15	3	0	0	0	0	N	1		
Fall	Sept. 1970				0	2	0	0	9	0	N	0	
Winter	Jan. 1971						110	110	N	0	0	0	2
Totals		116	5	15	3	2	110	119	0	1	0	0	2

<sup>a</sup>Data from two blocks only.



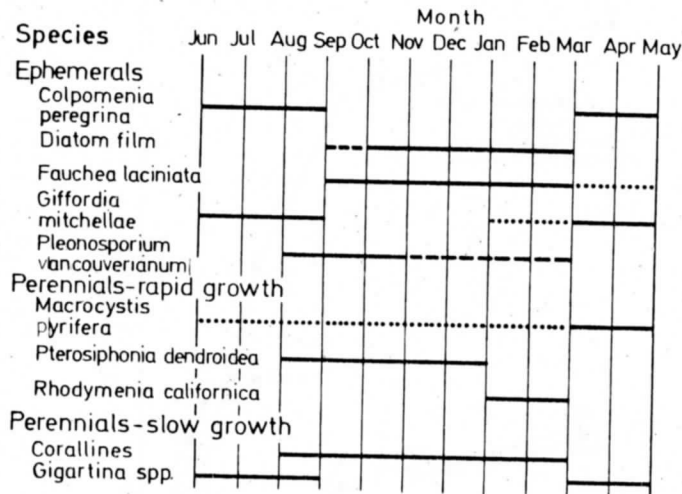


Fig. 5. Colonization times for the more abundant algal species. Solid lines indicate periods of maximum colonization; dotted lines, only slight colonization; dashed lines, possible colonization (data inconclusive)

in the surrounding community on the basis of weight, was never present in great numbers within the quadrats. Large numbers of small sporophytes did occur on some of the blocks (Table 3), but these plants were usually concentrated near the edges, outside the quadrats. The colonization period and growth of *M. pyrifera* was deduced from counts of young sporophytes on the sides and entire tops of the blocks (Table 3 and Fig. 6). As Table 3 shows, March through May are the months of maximum sporophyte production for this species, although some new sporophytes were found throughout the year.

In addition to seasonal differences in colonization, the elongation rates of particular algal species also influenced the successional patterns observed on the blocks. This influence was assessed using the branch length-measurements. Measurements from all 6 quadrats for a particular species at a particular time were combined and a mean length calculated. Lengths for filamentous species were estimated by measuring a few haphazardly selected individuals. All *Macrocystis pyrifera* and *Laminaria farlowii* on the blocks were measured. Because individual branches within the quadrats were not marked, successive mean lengths include previously measured branches as well as any new branches which grew up between sampling periods. This lowers the actual elongation rate but the effect is probably minimal for most species, since new colonization and basal

branch proliferation were generally not observed after perennial plants and animals began to grow and cover most of the available space.

Some plants were of considerable size when first encountered. Their initial settlement was estimated by extrapolating the elongation curves to the abscissa or, if this point came before the previous sampling date, by using the midpoint between surveys. *Macrocystis pyrifera* zoospore settlement was estimated at 60 days previous to the appearance of sporophytes (Neushul, 1963).

Graphs of length versus time for the more abundant plant species on each set of blocks are shown in Fig. 6. Excluding the *Macrocystis pyrifera* and *Laminaria farlowii* overstory, the relative lengths of the algae in the graphs are roughly indicative of their relative cover on the blocks, and can also be used as a crude indication of the stages observed during succession. As the graphs show, changes in composition are usually the result of differences in growth, not initial colonization. Most of the species present, whether ephemerals or fast or slow-growing perennials, can be early colonizers depending on the time of year space becomes available for settlement. *M. pyrifera* can be one of the earliest colonizers and can colonize with or precede *Giffordia mitchellae*. Articulated corallines, the most abundant plants on a bottom-cover basis in the surrounding community, can also be among the first organisms observed. The presence of the perennials was frequently obscured during the early successional stages by the rapid growth and cover of ephemerals. In general, the stages of succession observed on the blocks appear to be a result of differences in growth among the colonizing species rather than a result of "ecological" succession. *Gigartina* spp. and *Rhodomenia californica* may be exceptions, since they were generally not found earlier than 100 days after block placement.

To further test the growth versus "ecological" succession hypothesis, colonization on new and old blocks was compared. If some plants required the presence of others for colonization (excluding the obvious case of epiphytes), then they should occur in greater numbers on blocks which have been in place for some time. Table 4 compares colonization on old versus recently placed blocks on the same date for species other than *Macrocystis pyrifera*. Table 3 can be used for similar comparison of *M. pyrifera* settlement. To ensure that the comparisons reflected colonization and not growth of previously established indi-

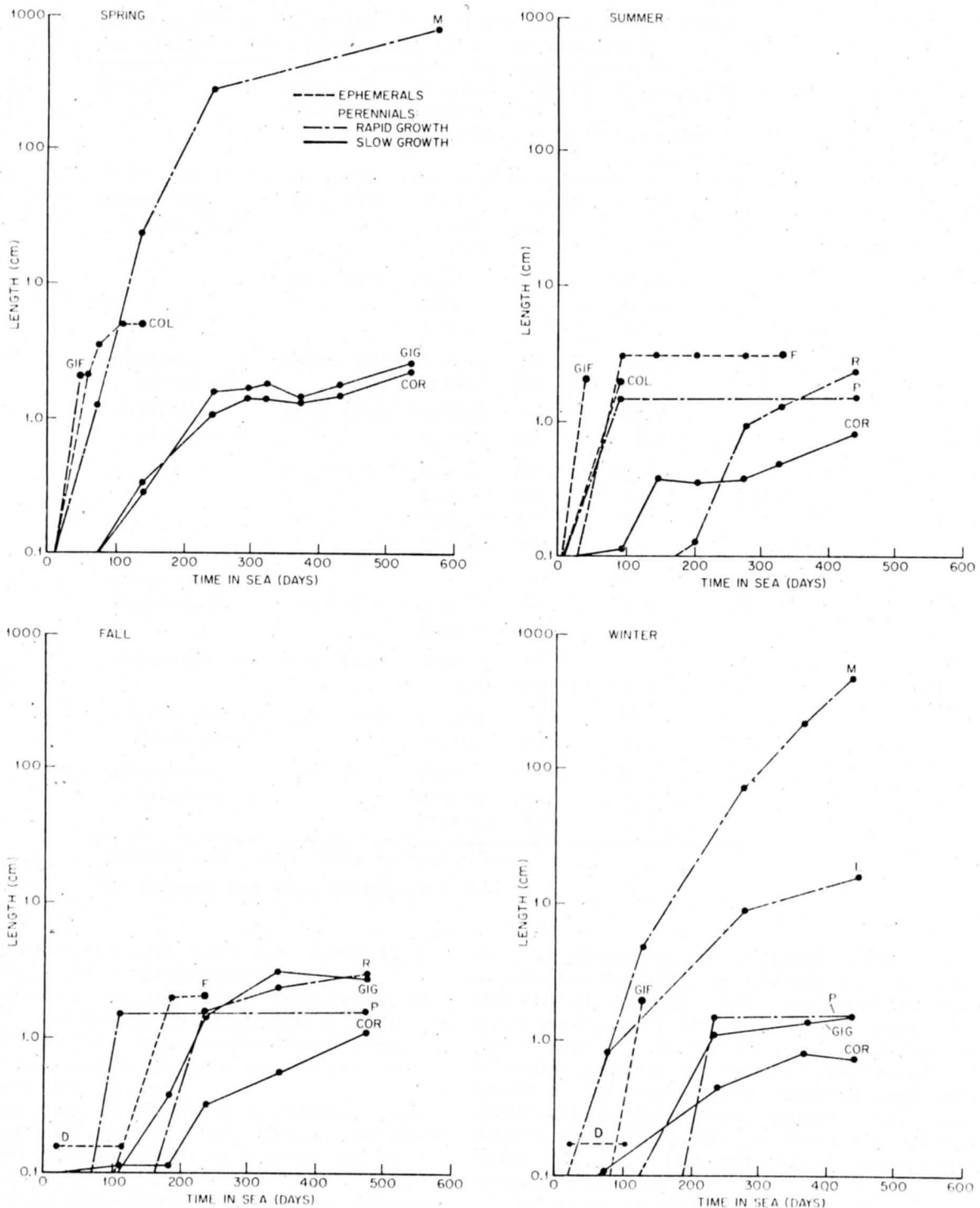


Fig. 6. Mean growth of the more abundant species found on the blocks. SPRING: blocks started 16 March, 1970; SUMMER: blocks started 25 June, 1970; FALL: blocks started 29 September, 1970; WINTER: blocks started 17 January, 1971. D: diatom film; COL: *Colpomenia peregrina*; COR: corallines; F: *Fauchea laciniata*; GIF: *Giffordia mitchellae*; GIG: *Gigartina* spp.; L: *Laminaria farlowii*; M: *Macrocystis pyrifera*; P: *Pterosiphonia dendroidea*; R: *Rhodymenia californica*. Diatom film lines (D) indicate presence only, not size. Measurements from all *M. pyrifera* and *L. farlowii* on blocks were used to determine their respective growth curves. Small sporophytes of these two genera were combined on the WINTER graph since they are indistinguishable. Growth curves for the other plants were constructed from measurements made on basal branches within the 20-cm<sup>2</sup> quadrats only. Lines which terminate before last analysis data indicate populations which stopped growing and began to decline during analysis period

Table 4. New colonization on recently placed versus older (on platform for longer time) blocks on same dates

Species	Date sampled	Season blocks placed	Time in sea (days)	% cover (%) or mean branches/20 cm <sup>2</sup>
Ephemerals	Nov. 1970	Fall	50	43.3%
Diatom film		Summer	146	0 %
		Spring	240	0 %
	Mar. 1971	Winter	73	80.0%
		Summer	279	0 %
		Spring	379	0 %
<i>Fauchea laciniata</i>	Sept. 1970	Summer	96	3.8
		Spring	197	0
<i>Giffordia mitchellae</i>	Aug. 1970	Summer	39	92.5
		Spring	140	3.0
	May 1971	Winter	126	47.5
		Fall	236	0
		Summer	332	0
		Spring	432	0
Perennials				
Corallines	Aug. 1970	Summer	39	1.5
		Spring	140	15.3
<i>Gigartina</i> spp.	Aug. 1970	Summer	39	0
		Spring	140	24.2
<i>Pterosiphonia dendroidea</i>	Aug. 1970	Summer	39	pb
		Spring	140	6.3
<i>Rhodymenia californica</i>	Jan. 1971	Fall	110	P
		Summer	206	3.3
		Spring	320 <sup>a</sup>	0

<sup>a</sup> Sampled one month later in Feb. 1971.

<sup>b</sup> P: Present but mean abundance < 1.

viduals, comparisons were not made if the plants had been present on old blocks during the previous analysis. In addition, comparisons in Table 4 were made only if the mean colonization on either old or new blocks was greater than 1 branch/20 cm<sup>2</sup>.

As the tables show, colonization of ephemeral species is much higher on newly placed blocks than on blocks with established communities of other organisms. Since the major difference between these blocks is the availability of space and light, established communities seem to inhibit colonization of ephemerals. The data for the perennials are not as clear. *Macrocystis pyrifera* was more abundant on new blocks, and *Rhodymenia californica* colonization was higher on blocks of intermediate age. *Pterosiphonia dendroidea*, corallines, and *Gigartina* spp. all colonized more heavily on older spring blocks. However, the reduced abundance of these species on the newly placed summer blocks may be the result

of the presence of *Giffordia mitchellae*. *G. mitchellae* density on summer blocks was very high at the time the comparisons were made, and the resulting lack of space and light reduction may have inhibited perennial colonization and growth. Moreover, the comparisons were made after the summer blocks had been in place only 39 days, perhaps too short a time for existing perennial germlings to attain visible size.

Sessile animals also settled on the blocks at all times of the year. They were not systematically identified and counted, but trends in their development were noted from occasional collections and close-up photographs of the blocks. They equaled or exceeded plant cover at certain times. Hydroids (*Obelia* spp. and *Plumularia* spp.), barnacles (*Balanus tintinnabulum*), and bryozoans were among the early colonizers, but the species present also varied with season. Tunicates and sponges were also found, generally later in time, but this may result from dif-

ferences in growth rates. The effect of these animals on algal colonization and growth was similar to the effect of the algae on each other. They occupied space which could have been occupied by plants, and the bryozoans, particularly *Parasmitina trispinosa*, were observed to grow over some of the young, slow-growing perennial plants (for further discussion of animal effects, see Foster, 1975).

### Diversity

Diversity ( $H$ ), number of species ( $s$ ), and evenness ( $J$ ) were calculated using the number of basal branches per species in each of the 6 quadrats from a set of blocks for each analysis date. The diatom film cover on fall and winter blocks was not included in the calculations. The resulting changes in diversity and its components with time, graphed using the means for each analysis date, are shown in the left column of Fig. 7.

Although there is much variability between the sets of blocks, certain trends are evident. Diversity generally rises to a peak between 100 and 200 days and then declines. The decline is associated with a drop in species on the spring and fall blocks, but is also correlated with fluctuations in evenness on summer and winter blocks. These fluctuations result from changes in the proportion of branches estimated for filamentous *Pterosiphonia dendroidea* and *Herposiphonia plumula* to those for other species present. *P. dendroidea* contributed over 80% of the total branches on the summer blocks at 440 days, producing the drop in  $J$  and  $H$  in Fig. 7 (SUMMER). Similarly, the drop in  $J$  and  $H$  at 361 days on the winter blocks resulted from *P. dendroidea* making up over 90% of the total branches. However,  $J$  tends to remain high after its early peak.

To test the significance of the apparent drop in  $H$  and  $s$  and the relative lack of change in  $J$ , the values of  $H$ ,  $s$ , and  $J$ , when  $H$  was at its peak on each set of blocks were compared with their values on the last sampling date on each set of blocks. Peterson (1972) has found that  $H$  and  $s$  are nearly normally distributed in southern California bivalve communities, and they appeared to be so in this study. However, evenness ( $J$ ) did not appear normal. To make the tests uniform, all parameters were tested with nonparametric Mann-Whitney U-tests. In addition,  $H$  and  $s$  were tested with a two-way analysis of variance (one way comparing the highest with the last samples, the other comparing seasons). The results of these tests are shown in

Table 5. The U-tests show that  $H$  and  $s$  are significantly less on the last sampling date. The difference in  $J$  was not significant. The results of the two-way analyses of variance were similar for  $H$  and  $s$ , and showed significant seasonal differences.

As a check on the adequacy of the quadrat size, all data for a set of blocks at a given time were pooled and  $H$ ,  $s$ , and  $J$  determined for this larger area (120 cm<sup>2</sup>). The resulting trends for these pooled data are shown in the right-hand column of the graphs in Fig. 7. The graphs are similar to those for the 20-cm<sup>2</sup> means, although  $H$  and  $s$  are higher. The spring and summer graphs are almost identical for the two quadrat sizes. Combining data for the fall blocks tended to magnify the effect of filamentous branches on  $J$  at 110 days, but the trend is similar after this. The slight drop in number of species for the small areas from the winter blocks did not occur in the large areas,  $s$  leveling off instead. The drop in  $J$  between 70 and 135 days for the winter blocks was a result of the combined effect of filamentous *Giffordia mitchellae* growth, and the drop between 240 and 361 days is associated with the growth of other filamentous species, as it was for the 20-cm<sup>2</sup> quadrats at the same time.

The rise and then decline of  $H$ , resulting primarily from similar changes in  $s$ , is directly related to the behavior of the various types of plants on the blocks. The rapid colonization by all types of plants produces the initial rise in  $s$ . The subsequent die-back of ephemeral species, combined with their general inability to colonize surfaces already occupied by established populations, resulted in the gradual decline and stabilization of species numbers. The relative size of the peak in  $s$  is related to the number of ephemeral species found on each set of blocks. The number of ephemerals (omitting diatom films) was: spring, 11; summer, 9; fall, 8; winter, 7. Spring blocks had the highest peak in  $s$ , followed by a distinct drop. On the winter blocks the peak in  $s$  was relatively small, and either dropped slightly or leveled off depending on the sample size.

### Discussion

The results of the study suggest that algal succession in this *Macrocystis pyrifera* forest is influenced by 4 major factors: (1) availability of new substratum for colonization; (2) species composition and abundance of reproductive ma-



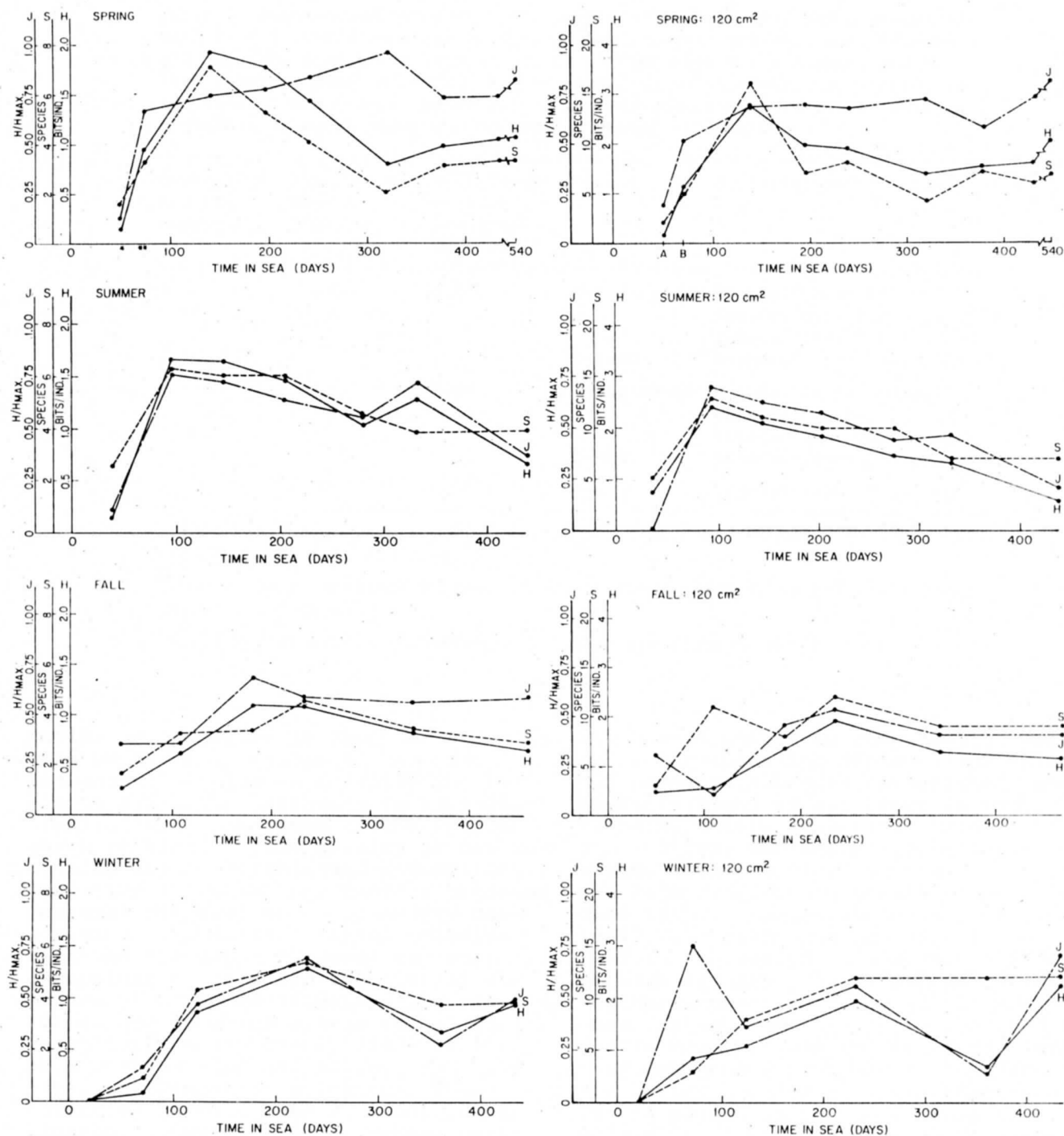


Fig. 7. Diversity ( $H$ , bits/individual), number of species ( $S = s$ ) and evenness ( $J$ ,  $H/H_{max}$ ) versus length of time blocks were in the sea.  $H$  and  $J$  were calculated using  $s$  and the number of basal branches (see text). Graphs in left-hand column are for 20-cm<sup>2</sup> quadrats and values are means of 6 quadrats unless otherwise noted (\* \*\*). Graphs in right-hand column are for 120-cm<sup>2</sup> areas (values calculated from pooled 20-cm<sup>2</sup> quadrats) unless otherwise noted. SPRING: spring blocks; SUMMER: summer blocks; FALL: fall blocks; WINTER: winter blocks. \*, means of 2 quadrats; \*\*, means of 4 quadrats; A: 40-cm<sup>2</sup> area; B: 80-cm<sup>2</sup> area

Table 5. Behavior of diversity ( $H$ ), number of species ( $s$ ), and evenness ( $J$ ) with time on the 4 seasonal sets of blocks. Comparisons were made between all quadrats from the 4 sets of blocks at time when  $H$  was highest and on last sampling date.  $H$ ,  $s$ , and  $J$  were tested using Mann-Whitney U-tests. In addition,  $H$  and  $s$  were tested with a two-way analysis of variance (using highest and last samples as one way and season as other)

Diversity and its components	Mean/20 cm <sup>2</sup> when $H$ highest <sup>a</sup> ( $N = 24$ )	Mean/20 cm <sup>2</sup> on last sampling <sup>b</sup> ( $N = 24$ )	Test	Significance <sup>c</sup>
$H$	1.495	0.834	2-way Anova	Highest-last: $P < 0.005$ Season: $0.01 > P > 0.005$ Interaction: $P > 0.1$ N.S.
			U-test	Highest-last: $P < 0.00003$
$s$	5.50	3.46	2-way Anova	Highest-last: $P < 0.005$ Season: $P < 0.005$ Interaction: $0.05 > P > 0.025$
			U-test	Highest-last: $P < 0.0001$
$J$	0.704	0.567	U-test	Highest-last: $P > 0.1$ N.S.

<sup>a</sup>Time when  $H$  highest (from Fig. 7): Spring, 140 days; Summer, 146 days; Fall, 183 days; Winter, 234 days.

<sup>b</sup>Time of last sampling: Spring, 540 days; Summer, 440 days; Fall, 472 days; Winter, 435 days.

<sup>c</sup>N.S.: Not significant. Differences judged significant when  $P < 0.05$ .

terial in the water at the time new substratum becomes available (assuming seasonal variation in colonization reflects a similar variation in reproduction); (3) growth rates of the species which settle; (4) the ability of new species to invade established communities. Variation in these four factors produces seasonal differences in community composition both during initial colonization and through subsequent succession. Exceptions to this are the initial enhancement of spore attachment by rapidly formed bacteria and diatom films (ZoBell and Allen, 1935; Scheer, 1945; Miller et al., 1948; Wood and Allen, 1950) and later settlement of epiphytes. These potential interactions were not investigated. Assuming that decreased perennial settlement on the new summer blocks was a result of the presence of *Giffordia mitchellae*, the indirect evidence from this study suggests that biological interactions during succession are negative (competitive).

Ephemeral species generally produced an early bloom on the blocks, obscuring or delaying the colonization of slower growing perennials. Ephemerals are opportunists in the sense of MacArthur (1960), characterized by rapid growth and rapid development of reproductive structures. Many ephemeral species,

which seem unable to compete with perennials for space and perhaps light after the perennials become established, are commonly found as epiphytes in the surrounding mature community. Established communities, whether early or later stages in succession, seemed to inhibit the colonization and growth of new species rather than enhancing it. "Ecological" succession was not apparent.

This conclusion is similar to those of both Kitching (1937) and Lee (1966). Further support is found in the work of Johansen and Austin (1970), who studied the *in situ* subtidal growth of the coral-line *Calliarthron tuberculatum*. The data of the latter authors indicate that substrata placed in subtidal areas where this alga is very abundant were almost immediately colonized by *C. tuberculatum*. The typical surrounding community was established immediately, with no early stages.

The combination of ephemerals with perennials produces the increase in diversity observed in the early phases of community development. The later decline of ephemerals and their inability to recolonize produces the drops in  $H$  and  $s$  (Fig. 7). They are thus "out-competed", and diversity drops as predicted by Margalef (1963). However, as Auclair and Goff (1971) have shown, diversity trends

in terrestrial forest succession vary with environmental gradients, and based on Paine's (1966) hypothesis, disturbance. Different trends may be found in *Macrocystis* spp. forests under different environmental conditions, particularly if these conditions affect the relative number of ephemeral versus perennial species.

Except for variations due to high numbers of filamentous branches on summer and winter blocks, evenness remained high during succession after its initial rise. Reiners *et al.* (1971) found that the evenness component increased with successional age in a terrestrial chronosequence in Alaska. Peterson (1972), studying bivalve communities in lagoons, found that a decrease in evenness was the best indicator of disturbance in this community. These results suggest that evenness may be a better indicator of relative maturity than either diversity or species richness.

After over 400 days, most of the blocks contained species which were rare or absent in the community survey adjacent to the platforms. In addition, corallines, the most abundant organisms on a per-cent cover basis in the surrounding community, were common only on the spring blocks (Table 2). These differences between the blocks and the surrounding community may be reduced if further growth of the perennial corallines results in their successful competition for space with other Layer 2 and Layer 1 plants. The mature composition may also be influenced by the long-term effects of differential grazing on fleshy species (Foster, 1975).

Based on the growth rates of the more common species and the lengths of these species in the surrounding community, one can speculate on the time-span of succession from initial colonization to maturity. On the basis of weight, *Macrocystis pyrifera* is the most common species. If the establishment of this alga is indicative of maturity, then succession takes about 1 year. The articulated corallines are most abundant on a percent bottom-cover basis, and might also be used as maturity indicators. On the blocks, they grew at a rate of between 1.1 and 2.2 cm/year. Surrounding plants of *Calliarthron cheilosporiodes* are 10 to 20 cm tall. Maturity based on the higher growth rate, assuming this rate is maintained, would thus be reached in 5 to 10 years.

The seasonal development of different algal communities observed in this study suggests mechanisms for the maintenance of diversity in the surrounding community similar to those found by Paine

(1966), Connell (1971), Dayton (1971), and Grigg and Maragos (1974) in other marine communities. Availability of relatively unoccupied natural substratum within the forest appears to result from changes in sediment cover, removal of plants during periods of heavy swell, and from removal of sessile animals by predators (Foster, 1975). Coches Prietos Cove faces south, and is exposed to refracted north swell in winter and direct south swell in summer. Therefore, all of the above mechanisms can create open space throughout the year. Thus, there is an opportunity for a variety of sub-communities or patches to develop within the mature community, each composed of somewhat different plants depending on when unoccupied substratum becomes available.

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